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Reptilian fossils from Windjana Gorge, Western Australia

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Abstract

A late Cainozoic lag gravel from Windjana Gorge contains the remains of a large crocodile and fragments of at least two chelonian genera. The distinctive ornamentation of some of these latter fragments suggest *Carettochelys*, a genus now restricted to New Guinea and the extreme north-eastern Northern Territory. The age of the fauna is difficult to assess but the presence of re-worked laterite pebbles suggest a post-Miocene age. If the deposit is correlated with the Warrimbah Conglomerate (Veevers & Wells, 1961) the age is no younger than Late Pleistocene.

Introduction

Reptilian fossils were collected from a Cainooic lag gravel on the north-western face of Vindjana Gorge, Western Australia (Fig. 1), luring 1972. Other Cainozoic vertebrate remains rom the area include *Diprotodon australis*, rom the bed of the Lennard River, downstream rom Windjana Gorge (Hardman 1884) and arge macropodine and crocodilian remains from a well at the "foot of St George Ranges, Cherraun Station, Fitzroy River" (Merrilees 1968). Glauert (1921) reported crocodilian and marupial remains from Quanbun Station in rocks hought to be of Pleistocene age. The associated marsupials are *Phascolonus gigas*, a large macropodine resembling *Protemnodon anak* and another large macropodine (Merrilees 1968).

Description of site

The fossils were recovered from a lag conglomerate deposited in, and adjacent to, a hallow cave in the northwest wall of Windjana Gorge, 900 m from the downstream end of the gorge and 41 m above the bed of the Lennard River. The cave is of no speleological significance but is typical of corrosion and solution eatures developed in vertical limestone cliff aces at or near river level (Jennings & Sweeting 963, p. 34). The conglomerate is poorly exposed and it is partly covered by limestone talus. As a result, the exact extent of the deposit is difficult to determine, but it is at least 2 m ong, 1.5 m wide and 1 m high. The deposit has been partly eroded. The contact between the onglomerate and the limestone is sharp but rregular. Where covered by the conglomerate he surface of the limestone appears to be mooth and resembles similar solution features developed at or just above the present river level. Exposed limestone surfaces are generally marked by rillen-karren structures.

The conglomerate is composed of rounded to subrounded quartz pebbles and subrounded to subangular quartz sand with minor amounts of mica, feldspar, and dark minerals. It contains rounded limestone cobbles as well as a few fragments of speleothem that apparently have fallen from the cliff face. The matrix is composed of limonitic clay and silt particles and part of the deposit is cemented by calcium carbonate. The uncemented portion is very friable but where cemented, fractures frequently break across quartz pebbles rather than around the margins of the pebbles.

Palaeontology

Class Reptilia
Subclass Archosauria
Order Crocodilia
Suborder Eusuchia
Family Crocodylidae
Genus **?Crocodylus**
?Crocodylus sp indet.

(Fig. 2A, B, C; Fig 3A, C.)

Material studied.—Incomplete left premaxillary fragment (CPC 17122), dermal scutes and fragmentary bones (Figs. 2A, B, C, 3A, C). The crocodilian remains were compared with remains of *Crocodylus porosus* (Fig. 2D) from the Northern Territory, material from Chinchilla and the Darling Downs, Queensland and from sites in Western Australia, cranial and scute remains of *Crocodylus johnsoni* (Fig. 3B) collected from the Lennard River, and illustrated material.

Premaxillary.—The fragmentary premaxillary (Figs. 2A, B, C) is 85 mm across at the widest point and exceeds 100 mm in length. The anterior part is missing and the posterior part is broken off behind the alveolus of the largest tooth. No teeth are in place, but fragments of the largest tooth (maximum diameter anterior-

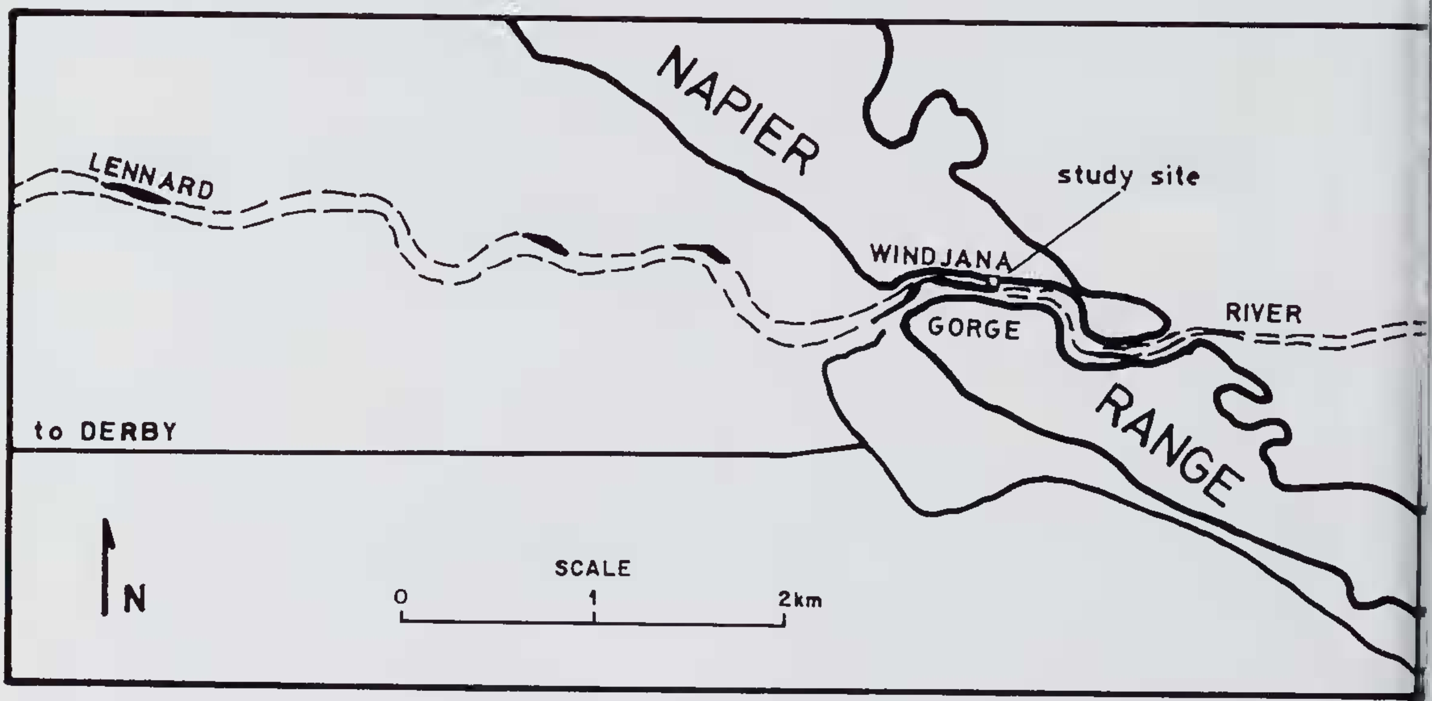

Figure 1.—Locality map showing the study site in Windjana Gorge. After the Lennard River 1 : 100 000 (Sheet 3863) topographic map.

posterior 29 mm) are cemented to the side of its alveolus. Anterior to the major tooth are alveoli for two more teeth, the posterior being the larger and the anterior being very much reduced. No alveolus is present for the posterior premaxillary tooth as the fossil is broken before the position of this tooth, but the tapering of the raised dental platform suggests that this tooth was very much smaller than the tooth immediately anterior to it. Comparison with the extant *Crocodylus porosus* (Fig. 2D) suggests that a fifth tooth was probably present at the extreme front of the snout just off-centre from the premaxillary suture. Thus the Windjana specimen probably had at least five, and probably no more than six, premaxillary teeth and differs in this respect from *C. porosus*, which has 4 premaxillary teeth (Iordansky 1973). The size differential of the teeth in the Windjana specimen serves to distinguish it from *C. johnsoni*, which has five teeth of similar size in the premaxillary (Woodburne 1967; Longman 1925a). Thus the fossil is distinct from both the extant Australian crocodiles.

The Windjana fossil was then compared to a small sample of fossil crocodilians and illustrated material. A fragmentary right premaxillary (QM F6123) from Chinchilla, Queensland, identified as *Pallimnarchus pollens*, is distinct from the Windjana fossil as the premaxillary probably bore more than six teeth. The Chinchilla specimen has five broken teeth in alveoli and one empty alveolus in the anterior portion; the anterior teeth and front of the premaxillary are missing. The general shapes of the two specimens, suggested by the preserved curvature of the outer surfaces, are distinct. The Windjana form probably possessed a blunter snout (brevirostrine), the outer bone surface curves strongly in front of the second largest tooth and the smallest tooth socket preserved is labially positioned just anterior of this tooth. Iordansky (1973) indicates that the largest teeth in both the upper and lower jaws lie in the central portions of the convex arches of the undulating jaw margins and reflect the pseudoheterodonty. Thus, conversely, the more marked the tooth size differentiation, the more pronounced the development of notches. In the Chinchilla specimen the line of the premaxillary immediately anterior of the largest tooth flexes slightly inwards but then straightens to run anteriorly, without a pronounced inward curvature: the snout probably tapered more than the Windjana form. The amount of curvature of the anterior part of the premaxillary on the Windjana form is reminiscent of that illustrated by Woodburne (1967 pl. 7 middle) as a probable juvenile right premaxillary of *Crocodylus* sp. from the Miocene and of *P. pollens* from Landsdowne illustrated by Longman (1925b, fig. 1).

The crocodilian described under the cabinet name of *Pallimnarchus pollens* (de Vis 1885) had a distinct premaxillary-maxillary notch similar to that described for *Pallimnarchus pollens* from Landsdowne Station (Longman 1925b). Projection of the snout curvature of the Windjana premaxillary suggests the animal was more allied to the short snouted (brevirostrine) crocodiles than other forms. The marked size differentiation of the premaxillary teeth of the Windjana fossil further suggests the form possessed a premaxillary-maxillary notch (cf. Iordansky 1973, p. 241).

Characteristics of crocodilian premaxillaries are compared in Table 1.

Scutes.—A fragmentary dorsal scute (CPC 17113); several fragmentary ventral scutes (CPC 17114).

Although all the scutes are very fragmentary t proved possible to reconstruct one dorsal and several ventral plates. Three features can be compared with known characters of other crocodilian scutes (Table 2). The dorsal scute (CPC 17113) can be distinguished from those of the Crocodylinae (except *Crocodylus johnsoni*, Fig. 3B), *Alligator* and the Gavials by the possession of an anterior bevelled margin which is overlapped by the smooth under surface of the preceding scute. The Windjana scutes may be distinguished from Alligatorinae scutes which are each composed of two parts united longitudinally by a suture (Kalin 1955). The possession of a longitudinal ridge on the dorsal scutes is characteristic of most crocodilians (Table 2) except *Alligator*, and this ridge is also lacking in the Windjana specimen. The Windjana specimen has serrated transverse sutures, a condition which rarely occurs in

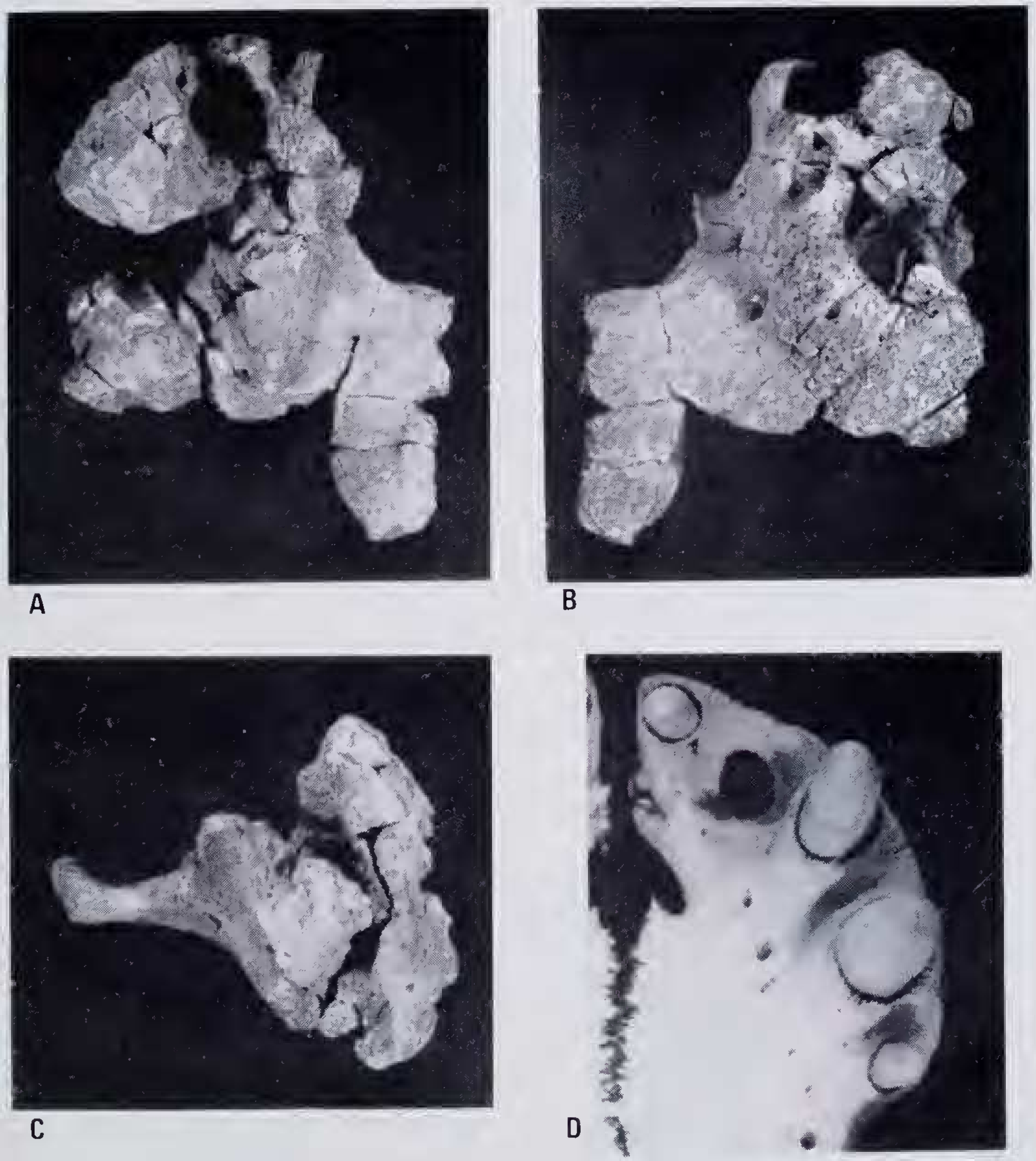

Figure 2.—A.—Dorsal view of left premaxillary fragment (CPC 17112), of *Crocodylus* sp. indet. from Windjana Gorge. x 0.75. B.—Ventral view of same x 0.75. C.—Frontal view of same x 0.75. D.—Ventral view of left palate of *Crocodylus porosus* from the Northern Territory (Specimen courtesy of R. Jenkins). x 0.75.

Alligator, Crocodylinae and Gavials, in which the scutes lie free in the integument (Kalin 1955). The possession of lateral sutures by the Windjana specimens ranks the fossil form with *Jacare, Caiman, Pallimnarchus* and *Crocodylus johnsoni* (a longirostrine form) and the Chinchilla specimens.

There is only slight angulation apparent on the dorsal scute, similar in degree of curvature to that on dorsal scutes of *C. johnsoni* examined, which serves to distinguish the scute from *Jacare, Caiman, Pallimnarchus* and the Chinchilla scutes.

Flat scutes (CPC 17114), similar in shape to scutes designated ventral by de Vis (1885), are present in the Windjana collection. These scutes, here identified as ventral scutes, do not possess crests or angulations, and also have an anterior bevelled edge and transversely serrated sutures, as in the Chinchilla scutes examined.

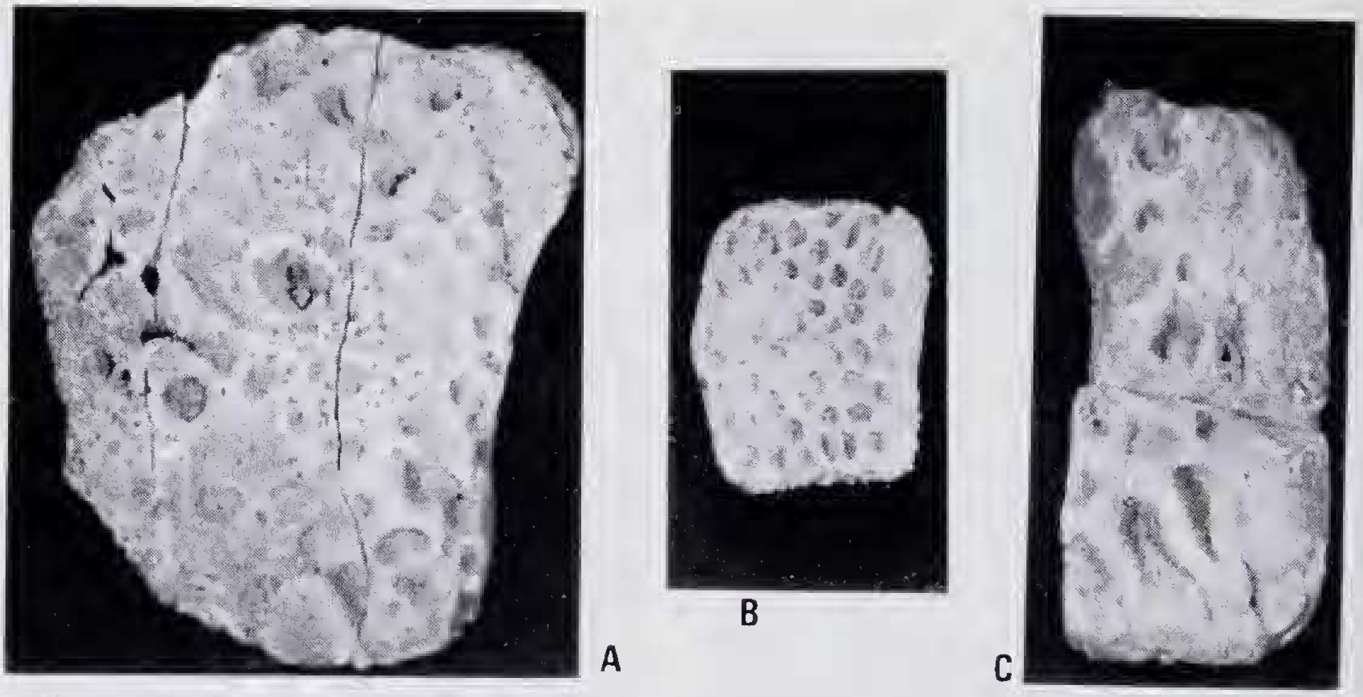

Figure 3.—A.—Dorsal scute of *Crocodylus* sp. indet. from Windjana Gorge (CPC 17113). x 1.0. B.—Dorsal scute of *Crocodylus johnsoni* from Windjana Gorge (CPC 17115). x 1.0. C.—Ventral scute of *Crocodylus* sp. indet. from Windjana Gorge (CPC 17114). x 1.0.

Table 1

Characteristics of crocodilian premaxillary and teeth morphology

	Number of premaxillary teeth	Pseudoheterodont	Medial mandibular occlusion	Notch	Tooth morphology	Ornament of teeth
Windjana premaxillary	?5 (4)	Yes	Yes	Yes	Rounded ?	....
Chinchilla premaxillary	+6	Yes	Yes	....	Sub-rounded ?	....
C. porosus	4 (3)	Yes	No	Yes	Sub-rounded	Smooth
C. acutus	5 (4)	Yes	No	Shallow	Sub-rounded	..
C. vulgaris	5 (4)	Yes	No	Yes	Sub-rounded	....
C. johnsoni	5 (4)	Slight	No	Shallow	Sub-rounded	....
P. pollens (de Vis, 1885)	5 (4)	Yes	?	Yes	Cylindrical, prominent anterior and posterior carinae	....
P. pollens (Longman, 1925b)	5 (4)	Yes	?	Yes	,, ,,	Minutely rugose on carinae
P. sp teeth (W. Australia)	.	...	...	....	,, ,,	,, ,,
Alligatorinae	5 (4)	Yes	Yes	No	....	....
Gavials	5	No, but 1st pm tooth strongest	No	No	Slightly curved and pointed	...

Data from: Huxley (1859), Kalin (1955), de Vis (1885), Longman (1925a), Longman (1925b), Iordansky (1973) and personal observations. Figures in brackets indicate number of largest premaxillary tooth.

Table 2

Characteristics of crocodilian scutes

	Lateral edges united by sutures	Anterior edge bevelled	Longitudinal ridge present	Angulation	Ventral scutes
Jacare	Yes	Yes	Yes	Yes	Yes
Caiman	Yes	Yes	Yes	Yes	Yes
Alligator	Rarely	No	No	No	No
Crocodylinae	Rarely	No	Yes	No	No
Crocodylus johnsoni	Yes	Yes	Yes	Yes	No
Gavials	Rarely	No	?	No	No
Chinchilla scutes	Yes	Yes	Yes	Yes	Yes
Pallimnarchus sp	Yes	Yes	Yes	Yes	Yes
Windjana scutes	Yes	Yes	No*	No*	Yes

* Only one dorsal scute in collection (CPC 17113).
Data from Huxley (1859), Kalin (1955), Longman (1925 a & b), de Vis (1885) and personal observation.

The possession of ventral scutes serves to distinguish the Windjana crocodilian from the Crocodylinae, *Crocodylus johnsoni*, *Alligator* and Gavials (Huxley 1859).

Thus on scute morphology alone, the Windjana crocodilian is distinct from the Crocodylinae and Gavials and seems to have more in common with the Alligatorinae (excluding *Alligator*) but to be distinct also from *Jacare*, *Caiman*, *Pallimnarchus* and the Chinchilla form. In the absence of more material it is impossible to place the affinities of the Windjana form more closely with any of the described crocodilians. An attempted diagnosis of the species is presented below.

Diagnosis: A brevirostrine form, with 5 premaxillary teeth, pseudoheterodont, a premaxillary-maxillary notch, mandibular teeth occluding inside the upper series, dorsal and ventral scutes, scutes without crests or angulations but having an anterior bevelled edge and laterally sutured edges.

The Windjana crocodile was a large animal. The recent specimen of *C. porosus* examined had a body length of just over 5 m (R. Jenkins, pers. comm.). By comparison of the size of the premaxillary of the *C. porosus* specimen and our Windjana fossil we estimate the length of our animal to have been about 7 m.

Order Chelonia
Suborder Cryptodira
Superfamily Carettochelyoidae
Family Carettochelyidae
Genus **Carettochelys** Ramsay
Carettochelys sp.
(Fig. 4C.)

Material studied.—Fragmentary plastron with ridged ornamentation (CPC 17118).

Carettochelyid turtles, characterised by *Carettochelys insculpta*, are at present found only in New Guinea and the extreme north of the Northern Territory (Cogger 1975). According to Ogilby (1905, p. 28, 29) the carapace and plastron plates are covered with "small, round, raised rugations or wavy irregular raised lines between shallow sculptures". The only other turtles having a similar ornament are the trionychids, represented in Australia by *Trionyx australiensis* described from Queensland (de Vis 1894). Gaffney recently re-examined the remains and corroborated the original interpretation (Gaffney 1976). The ornament is described as "irregular longitudinal ridges associated with generally weaker, less regular, transverse ridges giving pocketed appearance" (Hill *et al.* 1970, pl. Cz VII, fig. 8). The original drawing figured by de Vis (1894, pl. X) indicates that in *Trionyx* the ridges are thinner than the broadly sculpted intervening "valleys". This situation in *Trionyx* is the opposite of that displayed by the Windjana fossil (Fig. 4C), in which the ridges are broad and rounded and surrounded by intervening narrowly incised grooves, similar to the pattern described for *Carettochelys* by Ogilby (1905).

On the figured specimen, a pustular pattern is developed, suggesting that the fragment came from a more central part of the plate; towards the lower plate borders the ridges take on an elongated form parallel to the sutures (Ogilby 1905). The pattern on the specimen compares closely with that illustrated by Glaessner (1942, pl. X) of *Carettochelys* from Miocene deposits of New Guinea. Glaessner (1942, p. 107) described the ornament as "*Trionyx*-like granulation consisting of isolated small rounded or elliptical mounds separated by narrower or equally wide anastomosing depressions".

This distinctive ornamentation alone is sufficient to place some of the Windjana chelonians in the genus *Carettochelys*.

Suborder Pleurodira
Family Chelyidae
Genus **?Chelodina** Fitzinger
?Chelodina sp.
(Figs. 4A, B, F, G.)

Material studied.—Plastron fragments and unidentifiable bones, including a broken and waterworn right first pleural plate (CPC 17117), and a ?second left pleural plate, only the medial part of which is preserved (CPC 17116).

Comparison was made with known fossil and recent chelonians described in the literature and plates were orientated by reference to a carapace of recent *Chelodina longicollis* in the Bureau of Mineral Resources Palaeontological Museum.

First pleural plate.—The largest pleurodire fragment present in the collection (Fig. 4F) is an anterior right pleural plate (CPC 17117) which is both incomplete and waterworn. No surfical ornament is present, the posterior lateral mar-

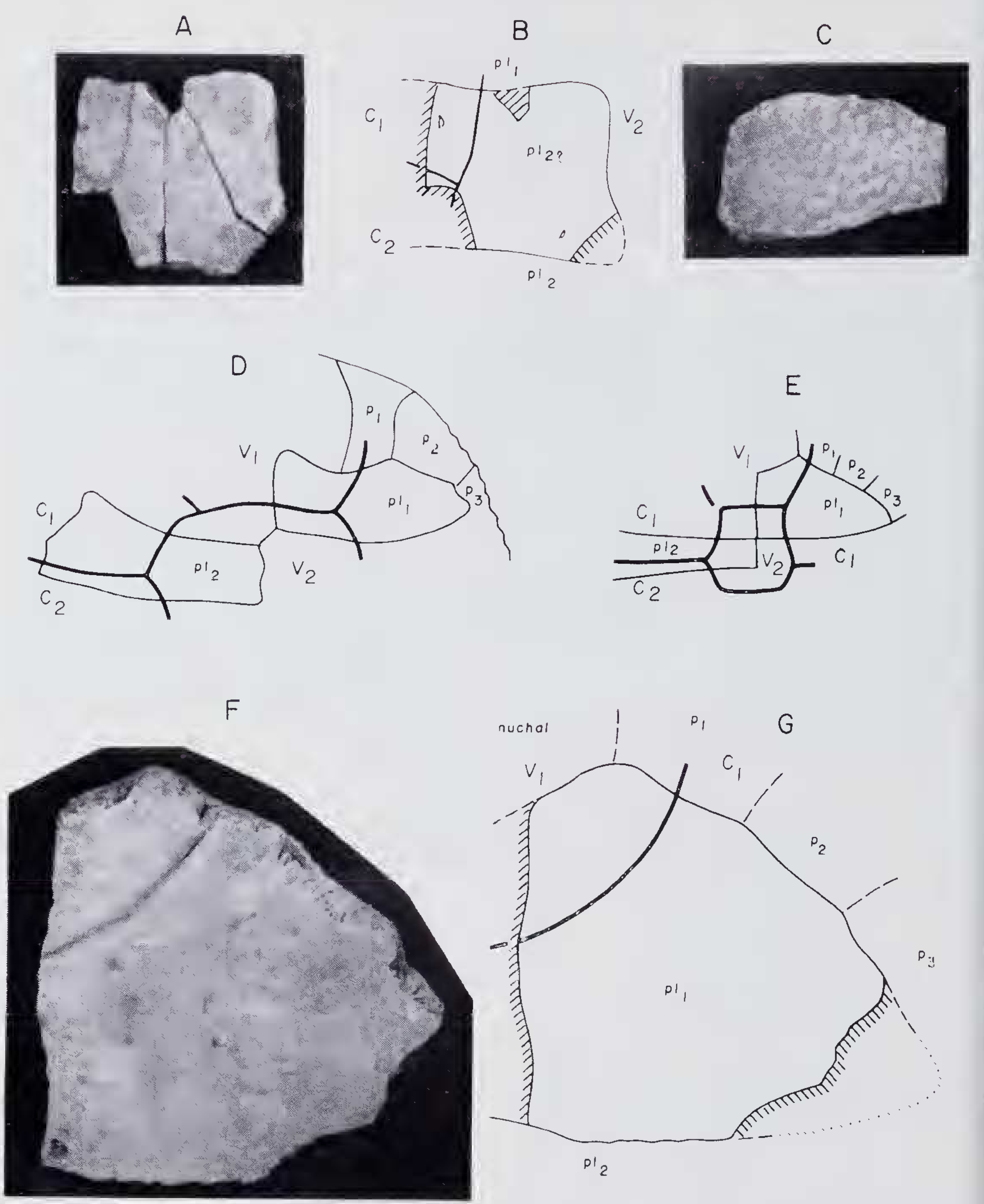

Figure 4.—A.—Dorsal view of ?left second pleural plate (CPC 17116) cf. ?*Chelodina* sp. from Windjana Gorge. x 1.0. B.—Sketch of same. C.—Fragmentary plate of *Carettochelys* sp. (CPC 17118) from Windjana Gorge. x 1.0. D.—Sketch of anterior dorsal carapace of *Emydura* sp. aff. *E. macquari* (after Warren 1969). E.—Sketch of anterior dorsal carapace of *Chelodina longicollis* (after Cogger 1975). F.—Right fragmentary first pleural plate (CPC 17117) of ?*Chelodina* sp. from Windjana Gorge. Dorsal view. x 1.0. G.—Sketch of same. Key: Heavy lines—trace of shield; fine lines—plate boundaries: pl_1—first pleural plate; pl_2—second pleural plate; p_{1-3}—peripheral plates; n—nuchal plates; V_1—first ventral shield; V_2—second ventral shield; C_{1-2}—first and second costal shields; diagonal shading—fracture.

gin is broken, and the medial portion of the plate is absent. The sutures for connection to the nuchal and three peripheral plates are present as is a partial suture with the second right pleural plate. In the anterior medial portion of the plate the trace of the join between the first vertebral shield and the first costal shield is present. This line rises on the border of the first pleural plate, probably about midway along the contact with the first peripheral plate, and swings posteromedially across the plate Fig. 4G). In *Chelodina longicollis* the triple unction formed by the meeting of the first pleural, first peripheral, and nuchal plates is anterior to this line (Fig. 4E) and the first plate forms a triangular shaped, forward oriented projection at this junction. In *Emydura* sp. aff. *E. macquari* (figured by Warren 1969) this triangular projection occurs at the join of the first and second peripheral plates and behind the first vertebral shield trace (Fig. 4D). The ateral margin of the fossil first pleural plate has a scalloped appearance and suggests that three peripheral plates adjoined it and in reconstruction (Fig. 4G) the trace of the first vertebral shield would cross onto the first peripheral behind the triple junction formed on the first pleural, first peripheral, and nuchal plates. Hence the affinities of the fossil are probably closer to *Chelodina* than *Emydura*. Comparison of the fossil plate with the recent specimen of *Chelonia* figured by Cogger (1975) excludes our specimen from that genus also.

The angle of the triangular projection, measured along a vector of the nuchal suture and a vector from the triple point junction to the join of the second and third peripherals at the lateral margin of the first pleural plate, is 120° on the recent specimen of *Chelodina longicollis* examined and approximately 135° on the fossil specimen. Comparison with other Australian forms such as *Pseudemydura*, *Elseya*, or the fossil horned turtle *Meiolania* were not made. In the absence of such comparisons the fossil is tentatively assigned to *?Chelodina* sp.

?Second pleural plate.—A fragmentary ?second left pleural plate (CPC 17116) is present in the collection (Fig. 4A). The medial suture is almost complete, but as only the medial part of the plate is present the sutures with the first and third pleural plates are only partly preserved. The trace of the junctions between the first and second costal shields and the second vertebral shields is present (Fig. 4B). The angle formed at the triple junction of these shields is more acute towards the anterior of the fossil and compares (Fig. 4B) more closely with this feature on *Chelodina longicollis* examined than with *Emydura* sp. aff. *E. macquari* figured by Warren (1969). However, as the variability of the shield traces is unknown to the authors, it is only tentatively accepted that this feature suggests affinities of the fossil with *Chelodina* sp.

Reptilian fossils from Jubilee Dam

We have examined fragmentary bone collected by K. McKenzie in 1960 from Jubilee Dam, about 11.2 km north of Quanbun Homestead in the Kimberley area (Merrilees 1968) and now lodged in the Western Australian Museum. The fossils, all numbered 60.10.10 consist of fragmentary crocodilian scutes, recognised by their characteristic ornamentation, one peg-like tooth, probably crocodilian and five waterworn pieces of bone. While one fragment has the characteristic cross-hatched pattern of the inner side of crocodilian scutes, other pieces are very similar in bone morphology to our *?Chelodina* fragments from Windjana Gorge. It is thus suggested that at least some of the fossil material collected by McKenzie is chelonian.

Depositional environment

The cave that contains the bone conglomerate was probably formed at river level. Similar karst features are now forming at river level in Windjana Gorge (Lennard River) and the nearby Geikie Gorge (Fitzroy River).

Deposition of gravel in the cave may have been roughly contemporaneous with cave formation or could have taken place at some later time during river flooding. The present-day Lennard River is depositing gravel only in the bed of the main channel and not on the banks. If we assume a similar flow regime at the time of deposition of the conglomerate, then the cave must have been at or near the level of the river bed, and the conglomerate represents the former level of the river bed.

The bone material is fragmentary, but much of this fragmentation appears to have occurred during weathering from the outcrop. Most of the bone fragments do not appear to be markedly abraded or waterworn, but partial skeletal disarticulation probably took place prior to deposition as there are no articulated bones present.

The remains of crocodiles and turtles in this deposit do not have any important palaeoenvironmental significance as both suborders occur in the nearby area. However, this new discovery would represent a significant range extension of *Carettochelys*.

The presence of the river turtle *Carettochelys*, at present commonly only in New Guinea, may imply a warmer climate in north-western Australia during the past, but without more evidence these conclusions are speculative. The amount of down-cutting of the Lennard River suggests that the river once carried appreciably more water at some time in the past, a conclusion consistent with the presence of the large crocodilian.

Age of the fossil deposit

Tertiary and Quaternary deposits are poorly known in the Kimberley area. Guppy *et al.* (1958, p. 63) gave the name Warrimbah Conglomerate to unconsolidated coarse gravels found 50 to 130 km downstream from Geikie Gorge in the Fitzroy River, about 25 m above the present flood plain (Jennings & Sweeting 1963, p. 13), Veevers & Wells (1961) have suggested correlation of the Warrimbah Conglomerate with high-level gravels at Windjana Gorge, from which a diprotodontid femur, collected by Hardman (1884), was thought to be derived. They suggested a Pleistocene age for both the Warrimbah Conglomerate and the high level gravels at Windjana Gorge.

The topographic height of the high level gravels at Windjana Gorge is not known but it is probable that the Lennard River has dissected several levels marking former land surfaces. As the reptile fossil site occurs in sediments 41 m above the river bed, it does suggest that these sediments would be among the oldest of any series of fluviatile deposit. Hence correlation with the Warrimbah Conglomerate gives a minimum age of Late Pleistocene for the fossils.

The presence of reworked laterite pebbles in the deposit suggests a post-laterite age. Lateritization in the Perth Basin has been dated as Late Oligocene to Early Miocene by Schmidt and Embleton (1976), although Playford *et al.* (1975) believe that most laterite in the basin is of Pleistocene age. Furthermore Playford *et al.* (1975) point out that whilst the period of lateritization in the Canning Basin is generally regarded as Tertiary, an Early Pleistocene age cannot be discounted. If Schmidt and Embleton are correct, and if lateritization was contemporaneous over the whole State, then the fossil site may be as old as Early Miocene.

On the basis of the fossils collected from Windjana Gorge no precise age can be affixed to the site and the conglomerate is too coarse and well oxidized to retain pollen. No mammalian remains were recovered from the site and it is therefore impossible to correlate the conglomerate with dated vertebrate sites elsewhere in Australia. However, some general comments can be made. *Carettochelys* is known from Miocene deposits in New Guinea (Glaessner 1942) and *Chelodina* ranges from ?Oligocene to Recent (Romer 1966). As the reference for the ?Oligocene age is not cited by Romer it is not possible to comment on the validity of this date. Accordingly, we have assigned the age of the Windjana fossil site as probably late Cainozoic.

Conclusions

Although the remains are very fragmentary, three distinct groups are recognized. These include an indeterminate crocodilian, a river turtle (*Carettochelys* sp.) and a pleurodire turtle questionably assigned to the genus *Chelodina*.

The presence of these fossils in the Windjana Gorge area may be evidence for a more humid climate during the late Cainozoic than the semi-arid one of today.

Acknowledgements.—We would like to express our thanks to R. Jenkins for providing the specimen of *Crocodylus porosus*, M. Archer of the Queensland Museum for the Chinchilla material, D. Merrilees of the Western Australian Museum for advice and Western Australian specimens and P. E. Playford for information on the elevation of the fossil site. The photographs were taken by R. W. Brown of the Bureau of Mineral Resources. All specimens are reposited in the Commonwealth Palaeontological Collection (CPC) at the Bureau of Mineral Resources, Canberra. This paper is published with the permission of the Director, Bureau of Mineral Resources.

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